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EUROPEAN CORN BORER REPRODUCTION: EFFECTS OF HONEY IN IMBIBED WATER

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ABSTRACT. European corn borer adults are well known to imbibe water, without which their reproduction is greatly decreased. Whether their reproduction is enhanced by sugars in imbibed water has long been unresolved. Two groups totalling more than 50 captive fertile pairs, one group receiving 15% honey-water to imbibe, the other plain water, were compared with respect to 10 reproductive attributes. Honey in imbibed water significantly improved performance in four attributes, resulting in heavier eggs, more females maintaining or increasing egg weight during the oviposition period, fewer females with immature oocytes at death, and more unlaid eggs that were mature. Adult nutritional ecology seems a potential factor in the dynamics of populations.

Additional key words: *Ostrinia nubilalis*, Pyralidae, Pyraustinae, fecundity, egg weight.

Imbibing of water by adults of the European corn borer, *Ostrinia nubilalis* (Hübner), is well documented (Vance 1949). Imbibed water greatly increases adult lifespan and fecundity; without it, reproduction is severely depressed (Barlow & Mutchmor 1963, Kira et al. 1969). Concerning sugars in imbibed water, reported effects are contradictory, one paper claiming no further improvement in reproduction (Caffrey & Worthley 1927), and another claiming the opposite (Kozhantshikov 1938). Unfortunately, the first paper offers no supporting data, and the second enumerates data insufficiently for independent assessment. Although this contradiction has never been addressed, the prevailing view, as reflected in mass rearing practice (Reed et al. 1972), is that sugars in imbibed water do not enhance reproduction. Clarification seems desirable for at least two reasons. First, European corn borer adults aggregate in grass and weedy vegetation bordering host fields (Showers et al. 1976), where potential adult food sources such as nectaries and honeydew-producing insects may occur. Second, if sugars do enhance reproduction, mass rearing programs might thereby increase production with little extra effort.

Here I report how European corn borer adults receiving honey-water and plain water performed in the 10 reproductive attributes listed in Table 1.

MATERIALS AND METHODS

One experiment was done. In it, 78 single female-male pairs of pupae were numbered, and the 39 even-numbered ones assigned to the treatment group, and the 39 odd-numbered ones to the control group. After adults eclosed, treatment pairs received honey-water to imbibe, control pairs plain water. After all moths had expired, reproduction data gathered from both groups were compared.

Pupae were obtained from a culture at the University of Minnesota originating in Iowa and maintained according to standard European corn borer production methods (Reed et al. 1972). The pupae were sexed, and pairs placed in 1-pint (0.47 liter) cardboard ice cream containers capped with Petri dish lids. Lids were lined with waxed paper to ensure a surface suitable for oviposition. Containers were kept in a walk-in environmental chamber programmed for 16 h light at 27°C and 8 h dark at 17°C, both at 60% RH.

Each container had a 35 cm^3 foam-latex sponge that dispensed distilled water in the control group and 15% (by volume) honey-water in the treatment group. Sponges and liquids were renewed every second day. Honey was used as the sugar source because in composition (White 1975) it conveniently simulates hexose-rich shallow-flower nectar (Baker & Baker 1983) and insect honeydew (Auclair 1963).

Reproduction data were gathered once daily near mid-day. Mating and fertilization success was ascertained by holding one or several early egg masses for a week or until the dark larval heads showed through chorions. Preoviposition period was measured from female eclosion to first oviposition; such data were used only when the male of the pair eclosed no later than one day after the female because late male eclosion prolonged the period.

"Early eggs" refers to eggs laid on the first or second day of oviposition, "late eggs" to eggs laid on the fourth to eighth day of oviposition. Mean egg weight was determined from one or more masses totalling 17 to 184 eggs removed intact from the waxed paper and weighed to the nearest 0.5 mg. Mature unlaid eggs were counted in excised ovaries at stereomicroscope magnifications up to 65×. Maturity of unlaid eggs was judged by size and chorionation. Eggs were deemed chorionated if they did not readily absorb 0.3% aqueous methylene blue after 3 min exposure (Jennings 1974). Immature oocytes in expired females could not be counted accurately, so only their presence or absence was recorded. Only data from fertile pairs were analyzed because some reproductive attributes are atypical in the absence of insemination.

Referral of species mentioned in this paper to Pyraustinae is based on the classification of Fletcher and Nye (1984).

Results and Discussion

Of the 78 pupal pairings, 79% resulted in fertile eggs, a level believed high enough to provide representative adult performance. Data were analyzed from fertile pairs numbering 25 and 27 in the plain-water and honey-water groups, respectively, these numbers also reflecting losses from mishaps like moth escapes. The fewest number of observations on any attribute in either group was 19 for preoviposition period in the water-imbibing control, reflecting a further loss of data on this attribute resulting from late male eclosions.

Four differences between the two imbibing groups were significant (Table 1). Thus, in the honey-water group, a greater proportion of unlaid eggs was mature, fewer expired females contained immature oocytes, late eggs were heavier, and more females maintained or increased egg weight during the oviposition period. The first and second differences suggest that honey-water imbibers approached full reproductive potential more closely than plain-water imbibers. The third and fourth differences presumably reflect conversion of glucose and fructose in honey to lipid that became incorporated into oocytes during egg maturation (Kozhantshikov 1938, Downer & Matthews 1976). Consequences of differing egg weights have not been investigated in the European corn borer, but in other moth species, heavier eggs produce larvae more likely to survive (Barbosa & Capinera 1978, Harvey 1985). Hence, sugars in imbibed water might enhance European corn borer fitness if females live long enough to lay the heavier eggs. Some do live long enough (Elliott et al. 1982): in 9 of 14 samples taken from June to September, $\frac{1}{6}$ of wild mated females were 4 or more days old, the onset age for heavier eggs in the present study.

Although 6 of the 10 reproductive attributes did not differ significantly between imbibing groups ($P \geq 0.06$, one-tailed Student *t*-tests), all attributes except female lifespan show differences of 1 to 150% in favor of the honey-water group (Table 1). Shorter female lifespan in the honey-water group seems anomalous, but no cause was evident. Despite this attribute, the honey-water group outperformed the plain-water group in an overall comparison of reproduction as follows. Of eight independent attributes (omitting number of unlaid mature eggs and percentage females maintaining or increasing egg weight, which are facets of other attributes), seven show gains resulting from honey imbibing whether individually significant or not, and such an outcome is not likely due to chance ($P < 0.05$, one-tailed sign test).

Because European corn borer fecundity varies directly with body size (Vance 1949), the possibility that body-size differences between imbibing groups caused attribute differences was examined. Vance (1949) did not express the relation mathematically; he tabulated six class means for number of eggs laid (y) and corresponding initial adult female weight (mg) (x). Based on retrospective frequency-weighted analysis of class means, the relation can be quantified as $y = 8.5x + 153$ (66n, $r^2 = 0.88$, $P < 0.001$). The correlation coefficient is overestimated because it is derived from means rather than individual values,

TABLE 1. Reproductive performance of European corn borer adults receiving plain water and 15% honey-water. Means and percentages are based on 19 to 27 observations per treatment group.

Attribute	Mean (±SD) or percentage		% change due to honey
	Plain water	Honey-water	
Lifespan, days			
Female	17.5 ± 5.4	16.5 ± 5.4	−6
Male	16.8 ± 4.0	18.2 ± 4.5	8
Preoviposition period, days	2.8 ± 1.3	2.3 ± 1.2	−18
No. mature oocytes			
Laid	601 ± 191	623 ± 237	4
Unlaid	28 ± 38	50 ± 53*	78
Total	630 ± 170	673 ± 209	7
% females containing immature oocytes at death	86	53*	−38
Egg weight, mg			
Early eggs	0.0638 ± 0.0048	0.0643 ± 0.0060	1
Late eggs	0.0618 ± 0.0066	0.0652 ± 0.0070*	6
% females maintaining or increasing egg weight	24	60*	150

* Significantly different ($P < 0.05$, based on one-tailed Student *t*-tests for means; 2 × 2 contingency tables and adjusted-G tests for numbers underlying percentages).

but the relation is nevertheless striking. Such a relation could not have affected attribute differences in the present study for two reasons. First, length of one forewing, a surrogate for body weight (Miller 1977), averaged 13.5 (SD ± 0.6) mm and 13.4 (SD ± 0.8) mm in females of the plain-water and honey-water groups, respectively. These means are identical statistically, the difference, 0.1 mm, being less than 1% of either. Second, in neither imbibing group did any egg attribute correlate significantly with female forewing length ($r^2 < 0.08$, $P > 0.20$).

In virgin European corn borer females, 80 egg follicles have been seen in one ovariole (Drecktrah & Brindley 1967). This number translates to 640 per female, near the average total number of mature eggs per female in the present study (Table 1). Number of oocytes already mature at female eclosion averaged 92 (SD ± 16, 4n) in the present study, as determined for females 0–4 h old averaging 14.0 mm in forewing length. Subtracting 92 from total mature eggs in the plain-water and honey-water groups leaves 538 and 581 eggs, respectively. The latter numbers suggest that more than 80% of oocytes mature after females eclose (538/630 = 0.85; 581/673 = 0.86), and that ample opportunity exists for adult nutrition to enhance oogenesis.

Although European corn borer adults have not been reported to imbibe sugary liquids in the wild, it is possible they do so opportunistically because adults of other Pyraustinae use such liquids. Both sexes of *Pyrausta orphisalis* Walker have been seen taking nectar from flowers (Campbell & Pike 1985). In *Cnaphalocrocis medinalis* (Guenée), imbibed sugars and planthopper honeydew greatly increased adult lifespan and fecundity (Waldbauer et al. 1980). Moreover, both sexes of European corn borer have well developed proboscides: females with forewing length (w) averaging 14.0 mm had proboscides with uncoiled length (p) averaging 7.3 mm (4n), forming a p/w ratio of 0.52. This length of proboscis could provide access to floral nectar of many kinds of plants, and the ratio is well within the range signifying flower visitation in other lepidopterans (Opler & Krizek 1984:31).

In conclusion, some differences in reproductive attributes between treatment groups are subtle. They nevertheless bring one step nearer resolution the old uncertainty whether sugars in imbibed water affect European corn borer reproduction. The adult's use of sugary liquids in nature remains to be shown. If it is shown, adult nutritional ecology could be a factor in the dynamics of populations, with sugar consumption perhaps elevating population quality and crop damage. Such an outcome could lead to removal of natural sources of sugar as a supplemental management technique for the insect.

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